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Otolith–fish size relationship in juvenile gag (*Mycteroperca microlepis*) of the eastern Gulf of Mexico: a comparison of growth rates between laboratory and field populations

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Abstract

In this study, we conducted experiments on wild-caught juvenile gag *Mycteroperca microlepis* from the eastern Gulf of Mexico to evaluate the effect of food availability on somatic growth and otolith growth. Juveniles were fed at two different food levels until all fish attained similar sizes. We found that food availability significantly affected growth rates. However, we also found that this manifested itself in differential otolith size. That is, slower-growing gag had larger, heavier otoliths than equal-sized faster-growing gag; an experimental result that has been observed previously among various fish species. We wanted to apply these experimental results to field-caught gag because our initial observations indicated that gag from more southern latitudes along Florida's west coast were larger than gag from more northern latitudes, at least during the early juvenile period. Applying these relationships to regional field populations, we found that juvenile gag from the more northern latitudes appeared to grow faster than those from southern latitudes, using an otolith–fish size proxy for growth. However, examination of fish length–age relationships revealed that juvenile gag growth rates were not significantly different between regions. These results are contrary to the expectation that larger-sized gag from southern latitudes are growing faster, and suggests that other factors, such as spawning time and habitat quality may explain regional size differences.
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Keywords: Gag; Grouper; Otolith growth; Somatic growth; Otolith size–fish size relationship; *Mycteroperca microlepis*

1. Introduction

Otoliths are used extensively in fishery studies to determine age, growth rates, and length–age relationships. Panella (1971) originally proposed the use of otolith microstructure for these purposes, under the assumptions that increments are formed daily, and that increment widths reflect somatic growth. That is, the

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greater the increment width between rings, the faster the growth rate. Many studies since have validated the formation of increments on a daily or near-daily basis, but the relationship between otolith size and body size to growth rate is not so simple. In fact, results from several studies (Bradford and Geen, 1987; Mosegaard et al., 1988; Reznick et al., 1989; Secor and Dean, 1986, 1989; Hovenkamp, 1990; Wright et al., 1990; Mugiya and Tanaka, 1992; Francis et al., 1993; Hare and Cowen, 1995) suggest that slower-growing fish may in fact have larger otoliths than faster-growing fish of similar sizes or ages. This is not intuitive, but it occurs because slower-growing fish have a higher ratio of mineral to protein in their otoliths, thereby producing heavier, thicker otoliths (Templeman and Squires, 1956; Radtke et al., 1985).

The intent of this study was to use the otolith–fish size relationship as a tool for evaluating inter-annual growth differences between populations of juvenile gag *Mycteroperca microlepis* (Goode and Bean) in the northeastern Gulf of Mexico (Gulf). Gag is a reef fish species whose juveniles settle in estuarine environments from the Gulf coast of Florida to North Carolina. Settlement occurs during April and May after an extended pelagic larval period (mean ~43 days, Keener et al., 1988; Koenig and Coleman, 1998). Juveniles experience rapid growth from June through August (>1 mm/day, Ross and Moser, 1995; Koenig and Coleman, 1998) and exhibit latitudinal differences in size along Florida's west coast shortly after settling in seagrass meadows. During settlement, seagrass meadows vary greatly in both quantity and quality (e.g., degree of epiphyte cover; Koenig and Coleman, unpublished data). Seasonal seagrass recovery also differs (due to winter die-off) and follows a latitudinal pattern (Zieman and Zieman, 1989). Maximum seagrass biomass occurs in April and May for southern latitudes and June and July for northern latitudes (Fitzhugh et al., unpublished data).

We presumed that regional differences in habitat quality would affect juvenile gag growth rates, and that differences in growth rate would explain regional differences in gag size. Latitudinal differences in growth have been observed for other species and can occur if the suitability of the environment for growth (e.g., food availability) changes with latitude (Conover, 1990, 1992; Conover and Present, 1992). Therefore, the objectives of this study were: (1) to determine experimentally how food availability, as a proxy of habitat quality, affects somatic and otolith growth; and (2) to use otolith–fish size relationships and fish size–age relationships to determine whether differences in size between regional populations of gag result from differences in growth rate. In addition, we hoped to develop methods for assessing growth rate more rapidly, and at lower cost than methods requiring analysis of otolith increments (Secor and Dean, 1989).

2. Materials and methods

2.1. Study sites

All juvenile gag were collected along the west coast of Florida from shallow (1–2 m deep) dense seagrass beds composed primarily of turtle grass, *Thalassia testudinum*. Collections for field studies came from three regions (Fig. 1), each representing a distinct faunal composition (Lyons and Collard, 1974; Hoese and Moore, 1998). The northern region (=Panhandle (PH), two sites) represented a warm-temperate area near the northwest extreme of seagrass habitat. This region receives no significant source of freshwater, has salinities ranging from 22 to 31‰, and temperatures ranging from 12 to 30 °C annually (Lott and Loftin, 1982). The mid-latitude region (=Big Bend (BB), four sites) represented a warm-temperate area and low-energy coastline lacking the protection of barrier

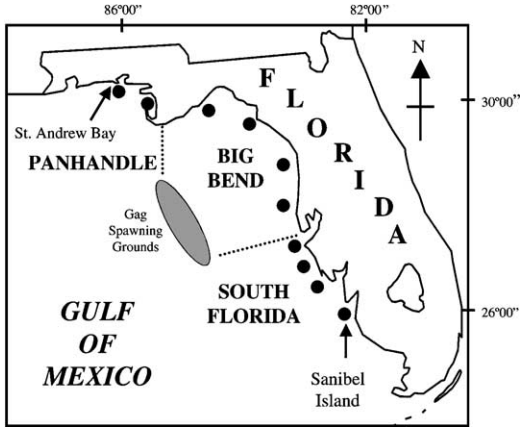

Fig. 1. Juvenile gag sampling sites and regions along Florida's west coast in the northeastern Gulf of Mexico. Regions are separated by dotted lines; dots indicate sampling sites.

islands. The southern region (=south Florida (SF), four sites) represented a semitropical area protected by beach-barrier islands, near the most southwest extent of seagrass habitat in Florida.

2.2. Sampling protocol

Juvenile gag were collected throughout the late spring and summers of 1992–1998 using either a 1 m wide benthic scrape with 3 mm-mesh bag (tow speed = 0.83 m/s for 50 m) or a 5 m wide otter trawl with 3 mm-mesh bag (tow speed = 0.50 m/s for 150 m). Sampling occurred twice each month and consisted of five tows made at each sampling site within each region. Fish were measured to the nearest mm standard length (mm SL), weighed to the nearest gram, and frozen for age and growth analyses. Fish for the experimental study were collected from the PH region in June of 1997 and were placed in an aerated tank and returned to the laboratory.

2.3. Length–frequency distributions of field-caught fish

Regional differences in fish size were examined using juveniles collected in June of each year (1992–1998) (Table 1). June samples were selected because this is the month during which settlement is completed (Keener et al., 1988; Koenig and Coleman, 1998). Although equivalent sampling occurred each year, the catch-per-unit-effort varied greatly between regions. A multiyear perspective allowed us to make inferences about size differences that may be consistent between regions, thus catches within each region were combined across years to increase sample size. For purposes of comparing length–frequencies between regions, we combined samples from both gear types; the fishing effort for each gear type was equivalent between regions.

Table 1
Total number of juvenile gag *M. microlepis* caught during June 1992–1998 from three regions in the eastern Gulf of Mexico[a]

Year	Sampling region		
	PH, *n*	BB, *n*	SF, *n*
1992	1	3	68
1993	–	14	11
1994	2	–	–
1995	13	14	30
1996	–	7	19
1997	32	7	14
1998	21	–	–
Total	69	45	142

[a] PH: northern latitude; BB: mid-latitude; SF: southern latitude; *n*: number of individuals.

2.4. Experimental design

Juveniles ($n = 30$) for the experiment were held in three aerated 380 l flow-through holding tanks. Several PVC pipes (200 mm long × 50 mm diameter) and oyster shells provided habitat structure in each of the holding tanks. Fish were initially fed live grass shrimp, *Tozeuma carolinense*, until they acclimated to eating in tanks. Fish were subsequently fed *ad libitum* measured portions of sliced penaeid shrimps weighed to the nearest 0.01 g. The amount of food consumed was recorded daily and consumption rates were calculated as a function of body weight. Mean (±S.D.) ad libitum food allotments were calculated as 0.25 g_{food}/g_{wt} per day (±0.17 g_{food}/g_{wt} per day).

After a 14-day acclimation period in the holding tanks, fish were distributed randomly among 30 flow-through (flow rate = 4 l/min) experimental tanks (76 l). One fish was placed in each tank. Each tank was provided with a PVC pipe and oyster shells, which served as habitat structure. The tanks were then covered with mesh to prevent fish from escaping. Tanks were cleaned twice weekly and three daily temperature, salinity, and dissolved oxygen readings were taken randomly among tanks. Temperatures during the experiment ranged from 27 to 31 °C (mean = 29.5 °C), salinity from 25 to 31‰, and dissolved oxygen from 6.0 to 6.2 mg/l (mean = 6.1 mg/l).

Fish were divided into two treatment groups, one receiving a high food (HF) allotment ($n = 15$) equivalent to one-fourth of their body weight (ad libitum), and one receiving a low food (LF) allotment ($n = 15$) equivalent to one-sixteenth of their body weight. Fish were fed once a day. During feeding, the submersible pump was turned off to avoid distracting the fish. Food was placed near habitat structure, and individual-feeding behaviors were recorded. Uneaten food was removed 2 h after each feeding.

At the onset of the experiment, each fish was weighed to the nearest gram and measured to the nearest mm SL. Experimental fish were measured every

2 weeks, but were not reweighed to avoid excessive handling. Rather, we determined weights based on length–weight relationships of field-caught juveniles ($n = 693$). The formula used was

$$\mathrm{Wt}=(2.0\times10^{-5}) \times \mathrm{SL}^{3.041}, \quad n = 693,\ r^2 = 0.98 \tag{1}$$

where Wt is fish weight in g and SL the fish standard length in mm. We then used the estimated weights to determine proportional increases in food allotments needed to adjust for growth.

The experiment ran for 9 weeks from 26 June through 28 August 1997. The HF experimental treatment ended after 6 weeks, while the LF treatment continued an additional 3 weeks to allow LF fish to achieve similar sizes as HF fish. All fish were sacrificed at the end of the experiment. They were then measured and weighed. A Student's *t*-test was used to compare final lengths and weights of HF and LF treatment fish. A repeated measures ANOVA was used to compare growth rates between treatments for the first 6 weeks of the experiment. Mauchly's sphericity test, using transformed dependent variables, was used to test the repeated measures ANOVA assumption of sphericity.

2.5. Otolith analysis for experimental and field-caught samples

Sagittal otoliths were removed from experimental and field-caught fish following the methods of Brothers (1987). Sagittal otoliths were removed from field fish collected only during June through August 1995, because this was the only year in which sufficient samples were available from all regions. By using only 1995 field samples, we were able to evaluate spatial differences in growth between gag populations, without confounding our results with potential temporal differences in growth rate.

Sagittal otoliths were viewed whole on a video monitor, digitized using image analysis software, measured along the longest axis to the nearest 0.01 mm, and weighed to the nearest 1×10^{-6} g. We preferred using sagittal otoliths rather than lapillus otoliths to develop otolith–fish size relationships because they were larger and allowed for less measurement error.

We tested for differences in the otolith–fish size relationship between the experimental fish from the two food treatments, as well as between the field-caught fish (60–150 mm) from the three regions using analysis of covariance (ANCOVA). An α level of 0.05 was used for all statistical tests, unless otherwise noted. When necessary, these data were log transformed to satisfy statistical assumptions of homogeneity of variance and normality. If the assumption of homogeneity of slopes was rejected when comparing regions, then three analyses of covariance (PH vs. BB; PH vs. SF; BB vs. SF; $\alpha = 0.016$) were used to test differences in slopes and *y*-intercepts.

2.6. Length–age relationships for field gag

Ages and growth rates were determined for field gag sampled during 1995 using lapillus otoliths. Lapillus otoliths are preferred over sagittal otoliths in age and growth studies because they are easier to grind, and more regularly shaped. Otolith processing and age interpretation followed the methods of Brothers and McFarland (1981) and Keener et al. (1988). Briefly, we selected the right or left lapillus from an individual fish and polished the otolith in the sagittal plane. After polishing, increment counts were made from the lapillus with a compound microscope (400×, 1000× magnification). Counts were made blind, without knowledge of location or region of the otolith sample. For purposes of the regional comparison, we assumed increments were formed daily following Brothers and McFarland (1981), Keener et al. (1988), and Brothers (personal communication, EFS Consultants, Ithaca, NY). We added six counts to the total increment count to establish fertilization dates. Six counts were added because lapillus otoliths in gag underestimate ages derived from sagittal otoliths by 4 days and increment deposition begins 2–3 days after fertilization.

We regressed size versus age, and used the slope of the line to estimate growth rate. ANCOVA was used to determine if growth rates varied significantly between sampling regions. The analysis included only those sizes that overlapped between the various regions (60–150 mm SL).

3. Results

3.1. Length–frequency distributions of field gag

Mean standard length increased from northern to southern latitudes for juvenile gag collected from the

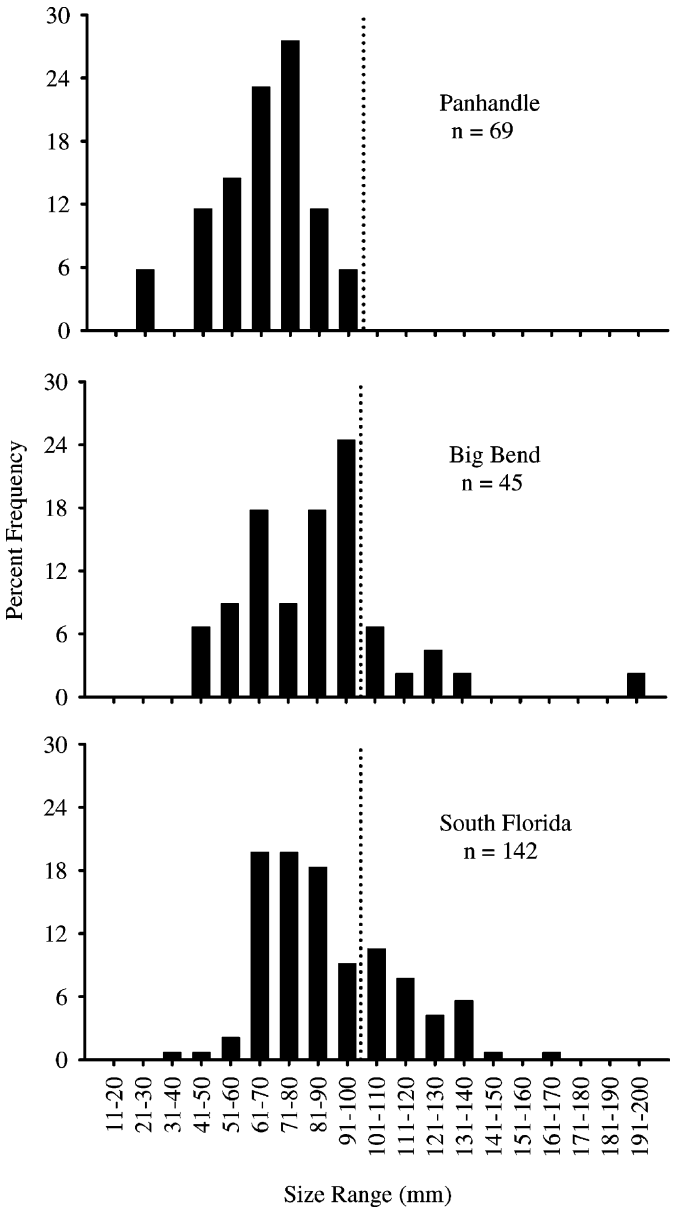

Fig. 2. Frequency distribution of juvenile gag standard lengths during June 1992–1998 from three regions in the eastern Gulf of Mexico. Dashed lines represent 100 mm SL.

west coast of Florida during June 1992–1998. Fish from SF (mean ± S.D. = 89 ± 16) and the BB (mean ± S.D. = 83 ± 22) were larger than those from more northern latitudes (mean ± S.D. = 66 ± 16) (Fig. 2). In fact, no fish were >100 mm SL in the PH, but 15% of BB fish and 24% of SF fish exceeded 100 mm SL.

3.2. Experimental fish

3.2.1. Fish growth

Growth rates for both HF and LF fish increased throughout the first 6 weeks of experimentation (Table 2). The HF fish had significantly greater

Table 2
Mean standard length, weight, food ration levels, and growth rates for juvenile gag fed on two different diets[a]

	Day 1	Day 14	Day 28	Day 42	Day 56	Day 63
(A) HF treatment						
n	15	11	10	9		
Mean SL (mm)	77.6 (±10.1)	90.0 (±11.7)	88.1 (±10.8)	100.1 (±12.2)		
Range (mm)	64–97	65–103	69–103	78–119		
Mean weight (g)	9.3 (±3.3)	13.7 (±5.8)[b]	16.9 (±5.8)[b]	25.6 (±9.1)		
Range (g)	4–16	6.5–26.5[b]	7.8–26.5[b]	10.9–41.9		
Average food amount per fish per day (g)	2.93 (±1.18)	3.42 (±1.45)	4.23 (±1.44)	–		
Range (g)	1.0–3.0	1.6–6.6	1.9–6.6	–		
Mean growth rate (mm/day)	–	0.55 (±0.40)	0.57 (±0.19)	0.93 (±0.31)		
(B) LF treatment						
n	15	15	15	15	15	15
Mean SL (mm)	77.3 (±12.8)	79.5 (±14.1)	85.7 (±13.9)	91.7 (±15.0)	100.1 (±15.9)	99.5 (±15.8)
Range (mm)	51–97	54–103	59–108	65–117	72–126	73–127
Mean weight (g)	9.1 (±4.6)	13.2 (±7.1)[b]	16.3 (±7.9)[b]	20.0 (±9.9)[b]	26.1 (±12.6)[b]	25.5 (±12.6)
Range (g)	2.0–19.0	3.7–26.5[b]	4.8–30.6[b]	6.5–37.0[b]	8.9–49.8[b]	13.4–48.9
Average food amount per fish per day (g)	0.57 (±0.29)	0.83 (±0.42)	1.01 (±0.49)	1.25 (±0.62)	1.63 (±0.78)	
Range (g)	0.1–1.2	0.25–1.6	0.3–1.9	0.4–2.4	0.55–3.05	–
Mean growth rate (mm/day)	–	0.24 (±0.23)	0.44 (±0.22)	0.43 (±0.15)	0.59 (±0.17)	0.05 (±0.15)

[a] *n*: number of individuals; standard deviation is given in parentheses.
[b] Estimated weights were calculated using juvenile gag catch data ($Wt = (2.0 \times 10^{-5}) \times SL^{3.041}$, $n = 693$, $r^2 = 0.99$).

growth rates than did the LF fish during this period ($F_{1,23} = 26.66$, $P < 0.001$, repeated measures ANOVA). The maximum mean growth rate for HF fish occurred by week 6 (=0.93 mm/day), approaching growth rates found in the field (~1.0 mm/day, Ross and Moser, 1995), and for the LF fish by week 8 (0.59 mm/day). At no time during the experiment did mean LF fish growth rates exceed those of the HF fish.

Five HF fish died, and one escaped during experimentation. Three died (one escaped) within the first 2 weeks, one by week 4, and one near the end of week 6 (Day 39). This last fish was included in the results because it exhibited a growth rate similar to other fish in the treatment. No cause of death for any fish was determined.

3.2.2. Otolith growth

Actual body weights of experimental fish did not differ significantly from estimated weights determined using the length–weight relationship ($P = 0.98$, Student's t, Eq. (1)). Body weights and standard lengths of experimental fish fed on low rations for 9 weeks were nearly identical to those of fish fed on high rations for 6 weeks ($P = 0.94$ and 0.82, respectively, Student's t). Despite these similarities in body size, we found significant differences in otolith size between fish reared at different food levels. Sagittal lengths were longer (9%) ($F_{1,23} = 32.66$, $P < 0.001$, ANCOVA) (Fig. 3) and sagittal weights were heavier (21%) ($F_{1,23} = 59.0$, $P < 0.001$, ANCOVA) (Fig. 4) in LF fish than in HF fish.

3.3. Regional otolith–fish size relationships

Sagittal lengths did not vary with fish size across regions (Fig. 5), whereas sagittal weights did (Fig. 6). In 1995, fish from northern latitudes had otoliths that were 9% lighter than equal-sized fish from southern latitudes (PH vs. SF: $F_{1,60} = 7.48$, $P = 0.008$, ANCOVA). Similarly, fish from mid-latitude sites had lighter otoliths at larger standard lengths (SL > 79 mm for SF; SL > 105 mm for PH) than fish from northern and southern latitudes (PH vs. BB: $F_{1,55} = 8.51$, $P = 0.005$, ANCOVA; BB vs. SF: $F_{1,80} = 10.71$, $P = 0.002$, ANCOVA). Otoliths from field-caught fish collected in the PH were also shorter (21%) and lighter (25%) than HF experimental fish (SL = 100 mm).

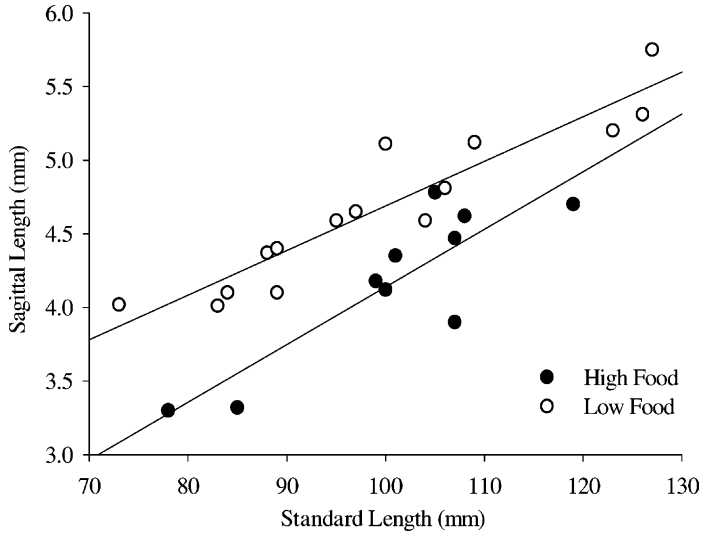

Fig. 3. Regressions of sagittal length vs. standard length for juvenile gag held under high and low feeding conditions (HF: $r^2 = 0.76$, SagL $= 0.039 \times$ SL $+ 0.225$, $n = 10$; LF: $r^2 = 0.87$, SagL $= 0.030 \times$ SL $+ 1.66$, $n = 15$).

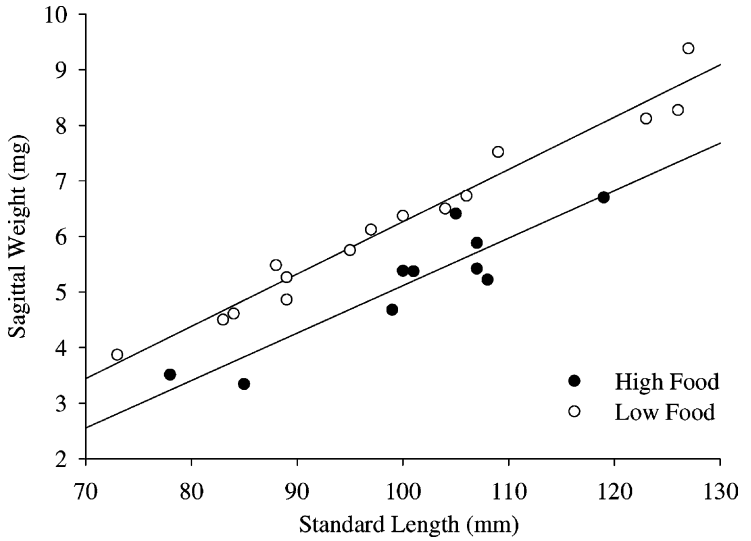

Fig. 4. Regressions of sagittal weight vs. standard length for juvenile gag held under high and low feeding conditions (HF: $r^2 = 0.84$, SagW $= 0.085 \times$ SL $- 3.42$, $n = 10$; LF: $r^2 = 0.96$, SagW $= 0.094 \times$ SL $- 3.14$, $n = 15$).

3.4. Length–age relationships

Length–age relationships (Fig. 7) for juvenile gag were not significantly different between regions ($F_{2,56} = 2.98$, $P = 0.06$, ANCOVA). When lengths were adjusted for age, there was also no significant difference in mean length-at-age between the three regions ($F_{2,58} = 0.41$, $P = 0.66$, ANCOVA). However, mean length-at-age (mm), and hence growth, was greatest in the PH (90.4 ± 3.3 SE) followed by the BB region (88.2 ± 2.7 SE) and SF (86.8 ± 2.4 SE).

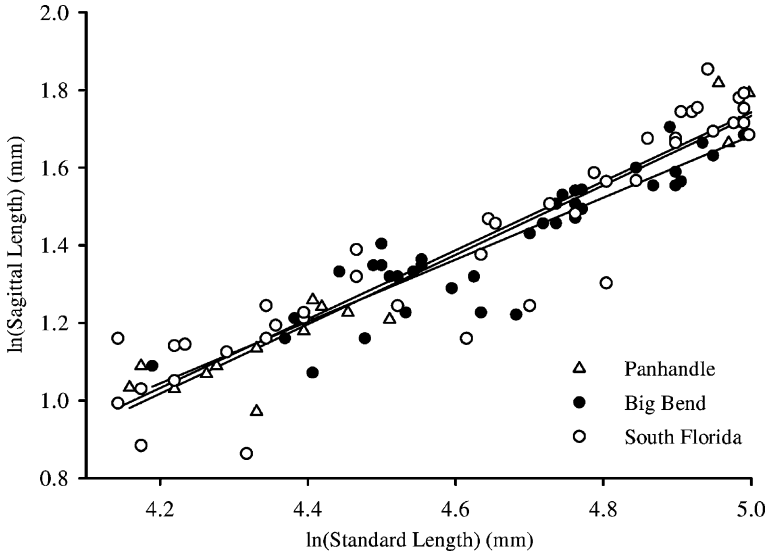

Fig. 5. Regressions of sagittal length vs. standard length for juvenile gag from three geographic regions in the eastern Gulf of Mexico (PH: $r^2 = 0.95$, $\ln(\text{SagL}) = 0.894\ln(\text{SL}) - 2.73$, $n = 19$; BB: $r^2 = 0.82$, $\ln(\text{SagL}) = 0.798\ln(\text{SL}) - 2.30$, $n = 40$; SF: $r^2 = 0.88$, $\ln(\text{SagL}) = 0.888\ln(\text{SL}) - 2.70$, $n = 44$).

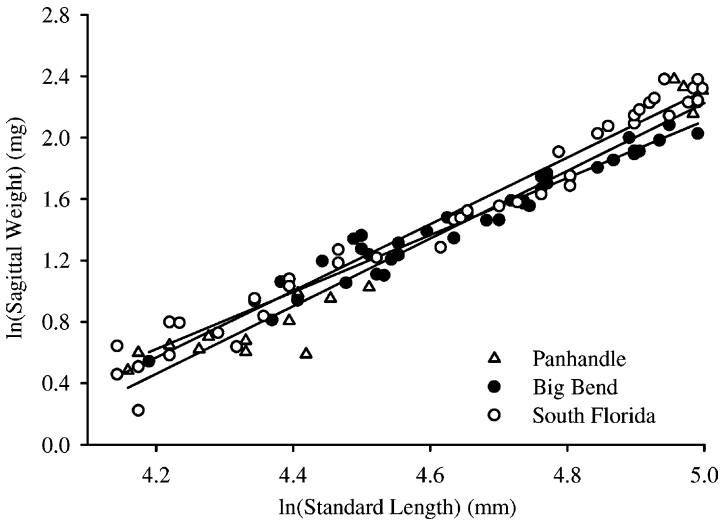

Fig. 6. Regressions of sagittal weight vs. standard length for juvenile gag from three geographic regions in the eastern Gulf of Mexico (PH: $r^2 = 0.96$, $\ln(\text{SagW}) = 2.20\ln(\text{SL}) - 8.80$, $n = 19$; BB: $r^2 = 0.95$, $\ln(\text{SagW}) = 1.85\ln(\text{SL}) - 7.18$, $n = 40$; SF: $r^2 = 0.97$, $\ln(\text{SagW}) = 2.17\ln(\text{SL}) - 8.85$, $n = 44$).

4. Discussion

Our experimental results suggest that differences in growth rate are detectable using the otolith size–fish size relationship. If true, then we can use this approach to develop an index of relative growth rate and an otolith size–fish size relationship that supplants and/or supports growth estimates obtained by more

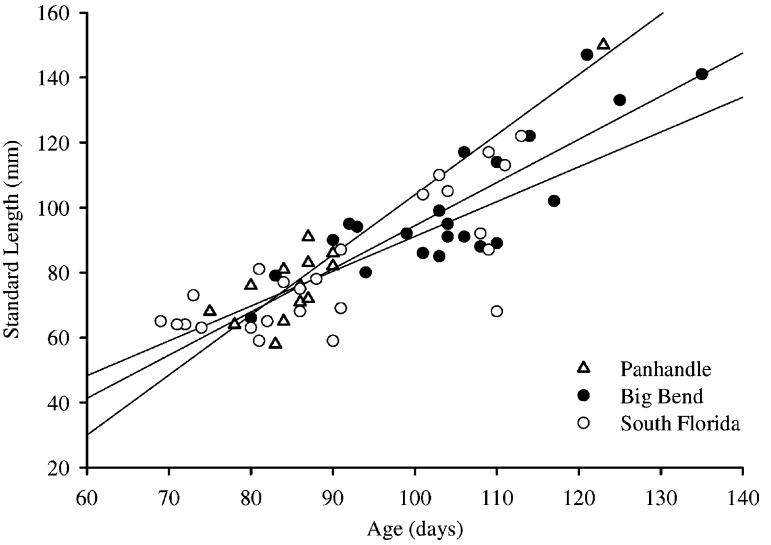

Fig. 7. Regressions of standard length vs. age for juvenile gag from three geographic regions in the eastern Gulf of Mexico (PH: $r^2 = 0.87$, SL = 1.849 × Age − 80.93, $n = 14$; BB: $r^2 = 0.69$, SL = 1.327 × Age − 38.37, $n = 23$; SF: $r^2 = 0.60$, SL = 1.07 × Age − 15.93, $n = 25$).

costly and time-consuming methods (Reznick et al., 1989).

Our success in detecting small regional differences in somatic growth using this relationship provides a basis for understanding what magnitude of differences in growth might be detectable in the field. For example, experimentally-induced differences in otolith size were much greater than those found in the field. Thus, there may be a trade off between sample size and magnitude of difference detectable in the otolith size–body size relationship. Differences of 21% (otolith weight), as observed in our rearing trial, were detectable with quite a small sample size and might represent an upper limit of about a twofold somatic growth difference. Our finding of smaller differences in the field (9% otolith weight) indicates that our sample sizes would need to be increased to detect more subtle habitat-based growth effects.

We found significant differences in otolith weights between laboratory and field populations. Otolith weights of HF treatment fish were 25% larger than otolith weights of field-caught fish of similar size (see Figs. 4 and 6), indicating that laboratory fish grew much slower than field gag. We attribute these differences in otolith size to tank induced stresses, handling, and food quality. However, these differences did not detract from the results of our field study. We were able to resolve small differences in somatic growth rate between wild populations, even when differences were smaller than those observed during rearing experiments.

We were also interested in knowing whether otolith length or otolith weight would be a more powerful indicator of differences in somatic growth. We assumed that otolith weight would be more accurate because otolith length measurements are compromised by high variability in otolith shape. Our rearing experiment revealed a much greater difference between HF and LF treatments in otolith weight (21%) than in otolith length (9%). Therefore, the power to resolve differences in growth rate was better for otolith weight. In fact, we did not detect differences between regions in otolith length–fish size relationships, but we were able to find differences between regions in otolith weight. Thus, otolith weight was a preferred indicator of relative growth difference.

Our intention was to use the otolith size–fish size relationship as a means of screening for habitat-related differences in somatic growth between wild populations (as suggested by Secor and Dean, 1986). Based on our catch data, differences in size–structure between regions exists shortly after settlement concludes

(∼early June, Koenig and Coleman, 1998, Fig. 2), with a greater proportion of large fish (>100 mm SL) observed in the south. Juvenile gag were much larger in SF estuaries and decreased in mean length with increasing latitude. That is, fish >100 mm SL were not collected in the PH during June in any year (1992–1998), whereas they were consistently collected every year in the BB and SF (see Fig. 2).

Since mean sea surface temperatures differ by only 1–1.5 °C between regions during late spring and early summer, differences in size were unlikely to be attributable to temperature. We expected these differences between regions to result from juvenile gag growing faster in more southern latitudes and that differences in fish growth rate resulted from variability in seagrass quality and quantity between regions. If this had been true, then otoliths from SF juveniles would have weighed less and been shorter than those from either the BB or the PH. However, this was not the case and our regional comparison of length–age relationships revealed no significant difference in juvenile growth rates; although the trend was for juveniles from the PH to be largest-at-age, followed by BB and SF gag (see Fig. 7). We suspect that other factors, such as latitudinal differences in spawning time and settlement, result in the observed differences in juvenile gag sizes.

We conclude that detection of somatic growth differences between field populations provides promise for the use of otolith size–fish size relationships as tools to screen for habitat-based differences in growth (as suggested by Secor and Dean, 1986). Estuarine environments play an integral role during early juvenile stages of many reef fishes, including gag (Keener et al., 1988; Ross and Moser, 1995; Koenig and Coleman, 1998), and it is critical to assess how quality and quantity of habitat affect fish population dynamics and productivity. Our finding of faster somatic growth in northern and mid-latitude gag (using otolith weight as a proxy) suggests that latitudinal differences in growth might exist, although more samples are needed. Our length–age relationships contradict these findings and suggest that latitudinal (regional) differences in gag size are not caused by differences in growth rate or seagrass quality. If growth differences do exist, then our findings have important implications for future studies of population dynamics, fish productivity, and stock assessment (Regner and Dulcic, 1994), especially considering that loss and degradation of habitat increasingly threaten the sustainability of coastal marine fishes (NMFS, 1994; Thayer et al., 1996; Waste, 1996).

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